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Patterns of selectivity in introductions of mammal species worldwide

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Abstract

Humans have an extremely long history of transporting and introducing mammal species outside their native geographic ranges. The characteristics of the species introduced (taxonomy, life-history, ecology, environment) can all influence which traits are available (and selected) for establishment, and subsequent invasive spread. Understanding the non-randomness in species introductions is therefore key to understanding invasions by alien species. Here, we test for selectivity in the identities and traits of mammal species introduced worldwide. We compiled and analysed a comprehensive database of introduced mammal species, including information on a broad range of life history, ecological, distributional and environmental variables that we predicted to differ between introduced and non-introduced mammal species. Certain mammal taxa are much more likely to have been introduced than expected, such as Artiodactyls in the families Bovidae and Cervidae. Rodents and bats were much less likely to have been introduced than expected. Introduced mammal species have significantly larger body masses, longer lifespans and larger litter sizes than a random sample of all mammal species. They also have much larger native geographic ranges than expected, originate from significantly further north, from cooler areas, and from areas with higher human population densities, than mammal species with no recorded introductions. The traits and distributions of species help determine which have been introduced, and reflect how the evolutionary history of mammals has resulted in certain species with certain traits being located in the way of human histories of movement and demands for goods and services. The large amount of unexplained variation is likely to relate to the intrinsically stochastic nature of this human-driven process.

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Keywords
Acclimatisation Societies, alien species, geographic range, introduced mammals, phylogenetic logistic regression models, taxonomic bias

Introduction

Humans have deliberately (and accidentally) transported a large number of species beyond the limits of their native distributions, to areas where they have subsequently escaped, or been released, into environments where they do not naturally occur (here termed introductions or introduced). Yet, these species are only a small fraction of those that could potentially be introduced. Given that introductions occur during the earliest stages of a process that leads, in some cases, to alien invasions (Blackburn et al. 2011), two particularly important questions are how many, and which, species are introduced? Here, we set out to answer these questions for mammal introductions worldwide.

Many studies have examined what proportion of the species in a taxon have been introduced, largely as a result of the influential Tens Rule proposed by Mark Williamson (Williamson 1993, 1996; Williamson and Brown 1986). Examples include angiosperms and Pinaceae introduced in Britain (Williamson 1993, 1996), fish, bird and mammal species introduced from Europe to North America (Jeschke and Strayer 2005), bird species introduced from North America to Europe (Jeschke and Strayer 2005), and amphibians introduced to Australia (García-Díaz and Cassey 2014). At the global scale, around 15% of parrots (54 out of *c.*350 species; Cassey et al. 2004), 10% of birds (973 out of *c.*10,000 species; Blackburn et al. 2015) and 3% of amphibians (179 out of *c.*6,000 species; Tingley et al. 2010) are known to have been introduced. Long (2003) provides accounts of 337 mammal species moved around the world (around 6% of the global mammal fauna), but some of this number have been re-introduced rather than introduced, while other mammal species with known introductions (e.g. *Callosciurus finlaysonii*, Bertolino and Lurz 2013) are missing from the compilation. A recent study by Capellini et al. (2015) identified 232 mammal species as having been introduced (*c.*4% of the total mammal species richness) based on data in Long (2003) and other sources.

Introduced species tend not to be a random subset of the species in a taxon. This has been studied most extensively for birds (Blackburn et al. 2009). Among birds, species from taxa favoured as game and cage birds occur more often than expected by chance in lists of introduced species (Blackburn and Duncan 2001; Duncan et al. 2006; Blackburn and Cassey 2007; Blackburn et al. 2010). At the global scale, Nearctic and Palaearctic species are also over-represented, and this translates into a tendency for introduced species to derive from latitudes in the northern hemisphere (Blackburn et al. 2009). Introduced birds tend to be species affiliated with humans (e.g., commensals, cage-birds, and food species), widespread and abundant, and large-bodied and long-

lived (Blackburn and Duncan 2001; Cassey et al. 2004; Jeschke and Strayer 2006; Blackburn and Cassey 2007; Blackburn et al. 2009, 2010). This suggests that introduction is an outcome of the interaction between human socio-economic pressures (e.g., for food and pets) and species availability for these uses (e.g., common species in areas where socio-economic demands have historically been high).

Similar patterns of selectivity have been shown in other taxa. For example, introduced fishes show a strong taxonomic bias towards game or forage fishes, or other species of human interest. They are also often piscivorous (Garcia-Berthou 2007). At the global scale, introduced amphibians tend to originate from the Northern hemisphere, to have broad geographic ranges, and to be sympatric with high densities of humans (Tingley et al. 2010). Amphibian introductions to Australia were more likely for species imported both accidentally and for trade (rather than by one or the other pathway), and for larger-bodied species (García-Díaz and Cassey 2014). Taxonomic non-randomness and large body size were features of reptiles introduced to South Africa (van Wilgen et al. 2010). Through analysis of fish, bird and mammal introductions between Europe and North America, Jeschke and Strayer (2006) found that introduction was more likely for widespread, human-affiliated fish with large eggs, and long-lived, herbivorous mammals. When fish, birds and mammals were analysed together, human affiliation, wide latitudinal range and body mass were all significant predictors of introduction (Jeschke and Strayer 2006). At the global scale, introductions have been shown to be more likely for mammal species with larger and more frequent litters, and longer reproductive lifespans (Capellini et al. 2015), although this study only analysed body size and life history traits related to reproduction.

Here, we build on these previous studies, exploring the number and characteristics of introduced species, using a global database of mammal introductions. First, we quantified and characterised the taxonomic distribution of introduced mammal species, to reveal which orders and families of mammals have more (or fewer) introduced species than expected by chance. As far as we are aware, this is the first study to identify non-randomness in the taxonomic distribution of introduced mammal species worldwide. We then tested for non-randomness in a range of characteristics that previous studies have shown to be associated with introduction selectivity, and which may help explain why certain taxa are over or under-represented in the list of introduced mammals. Specifically, we tested whether mammal species that have been introduced somewhere in the world differed in measures of (1) body size, (2) fecundity, (3) lifespan, (4) ecological generalism, (5) herbivory, (6) geographic extent, (7) human population density across their geographic ranges, and (8) location of their native geographic range, compared to mammal species that have not been introduced. The specific hypotheses tested are given in Table 1. Previous studies have considered subsets of these characteristics (e.g. Capellini et al. 2015) or regional introductions (Jeschke and Strayer 2006), whereas this is the first test of such a range of hypothesised associations at the global scale.

Table 1. The characteristics of species that we expected to influence whether or not mammal species have been introduced, based on patterns of selectivity shown in other taxa (see Introduction for more details), the specific hypotheses associated with those characteristics, the specific variables analysed (with sample size) and a description of that variable (see Methods and Jones et al. (2009) for more details).

Characteristic	Hypotheses	Variable (sample size)	Description
Body size	We expect utilitarian species (e.g., food and pack animals) to be more likely to have been transported and introduced, and therefore that introduced species will be larger than expected by chance.	Adult body mass (3,542 species)	Grams (log transformed)
Fecundity	Species with relatively slow life histories may be more likely to be utilitarian species (and so also have large body size) and better able to survive the introduction process. Alternatively, species with faster life histories may be more likely to maintain populations through the stresses of transport and introduction.	Litter size (2,502 species)	Number of offspring born per litter (log transformed)
Lifespan	Species with relatively slow life histories may be more likely to be utilitarian species (and so also have large body size and low fecundity) and better able to survive the introduction process.	Maximum Longevity (1,013 species)	Months (log transformed)
Ecological generalism	Generalist species may be more widespread and abundant, more easily kept in captivity, and more flexible in their ability to cope with the demands of transport and introduction. Thus, introduced species are more likely to have generalist diets.	Diet breadth (2,161 species)	Number of dietary categories used by a species
	Generalist species may be more widespread and abundant, more easily kept in captivity, and more flexible in their ability to cope with the demands of transport and introduction. Thus, introduced species are more likely to be habitat generalists.	Habitat breadth (2,724 species)	Number of habitat layers used by a species
Herbivory	We expect utilitarian species (e.g., food and pack animals) to be more likely to have been transported and introduced, and therefore that introduced species are more likely to be herbivores.	Trophic level (2,161 species)	1: herbivore (not vertebrate and/or invertebrate prey): 2: omnivore (vertebrate and/or invertebrate prey plus any of the other categories); 3: carnivore (vertebrate and/or invertebrate prey only)
Geographic extent	Species with a greater native distribution (which tend also to be abundant) will be more available for deliberate or accidental transport and introduction.	Geographic range size (4,668 species)	Area of the native range in km^2 (log transformed)
Human population density	Introduced species tend to be those affiliated with humans. Such species may be more likely to be found in areas with greater concentrations of humans and human activities, and will be more likely to be deliberately or accidentally transported and introduced as a result.	Human population density (4,668 species)	Average number of persons per km^2 within the native geographic range (log +1 transformed)
Location of the native geographic range	Many introductions have been associated with colonial expansion of European countries, primarily to Neo-European colonies at similarly high latitudes. We therefore expect introduced species to be more likely than expected by chance to derive from higher latitudes.	Latitudinal mid-point of the geographic range (4,668 species)	Degrees of latitude, with negative values indicating mid-points south of the equator
	Many introductions have been associated with colonial expansion of European countries. We therefore expect introduced species to be more likely than expected by chance to derive from European longitudes.	Longitudinal mid-point of the geographic range (4,668 species)	Degrees of longitude, with negative values indicating mid-points west of the Greenwich Meridian
	Rainfall tends to be higher in tropical areas that have been less associated with European colonial expansion. We therefore expect introduced species to be less likely than expected by chance to derive from high rainfall regions.	Mean precipitation (4,533 species)	Mean monthly precipitation (mm) within the geographic range (log transformed)
	For the same reasons as latitude, we expect introduced species to be more likely than expected by chance to derive from areas with lower mean temperatures.	Mean temperature (4,533 species)	Mean monthly temperature (°C) within the geographic range

Methods

Data

We compiled a comprehensive database of mammal species introduced to areas beyond the limits of their historically recognised native geographic ranges. The starting point for our database was the compilation of mammal introductions by Long (2003). Each species listed by Long (2003) was then subjected to a primary literature search to verify or update these classifications using Google Scholar, with the search terms 'introduced OR alien OR exotic OR invasive OR native' and the species' common and scientific names. We also conducted specific searches including the names of potential geographic locations of introduction identified in Long (2003). We searched the following online databases to determine the status of the species recorded in Long (2003): the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, Delivering Alien Invasive Species Inventories for Europe (DAISIE) and the Invasive Species Specialist Group (ISSG). These online databases, together with general Google Scholar searches using the search terms 'introduced OR alien OR exotic OR invasive OR native AND mammal AND Country Name/Region', were used to identify introduced species omitted from Long (2003), either because he had missed the evidence or the introduction post-dates his work.

Species were considered to be introduced when there was evidence that individuals arrived into an environment via human mediation, except when there was evidence that the liberated or escaped populations were to sites within the historic range of the species (i.e., re-introductions). Native ranges were determined from a combination of IUCN distribution maps (IUCN 2014), the Handbook of Mammals of the World (Wilson and Mittermeier 2009, 2011; Mittermeier et al. 2013) and primary literature. There were a number of species in our database for which it was unclear whether or not introductions had actually taken place (e.g. *Leopardus tigrinus*; Long 2003). We excluded these species from further consideration. We cross-checked our compilation with that of Capellini et al. (2015), and in some cases amended our classifications to align with theirs; we did not always concur with their classifications, however (see Discussion). We also excluded species not considered to be valid according to the taxonomy we used (Wilson and Reeder 2005). A full list of introduced mammal species in our analysis is provided in Table S1 in Suppl. material 1, and the references used to build this list in Suppl. material 2.

We obtained data on a range of life history and geographic variables for a large sample of mammal species from the PanTheria database (Jones et al. 2009), where more details of sources and calculation are provided. We used the version of the database based on the taxonomy of Wilson and Reeder (2005). The geographic variables were all calculated from digital geographic range maps of all extant, non-marine mammals from Sechrest (2003), converted to this taxonomy. PanTheria sometimes includes multiple variables relating to the characteristics of interest in our analyses. In such cases, we selected variables that measured different facets of that trait (e.g. dietary and habitat

generalism), but only if they were available for a reasonable number (at least 40%) of species. The only characteristic that did not meet this sample size criterion was lifespan: for this trait, we used the variable with the largest sample size instead (Maximum longevity: 18.7% of species). Excluding variables with few data may mean that some traits associated with introduction are missed by our analysis. On the other hand, ensuring that we have data for a high proportion of mammal species reduces the likelihood of spurious relationships based on small and biased samples. We have generally excluded variables that are correlated with those we included so that in most cases we should capture variation in the relevant characteristic. The 12 variables associated with the eight characteristics of interest (and associated sample sizes) are provided in Table 1. Correlation analysis shows that these variables are generally weakly related ($r < 0.34$ for 30/36 pairwise correlations); the exceptions are correlations of log litter size to log mass ($r = –0.43$), log lifespan to log litter size (–0.58) and log body mass (0.66), and of mean temperature to log litter size (–0.42), log precipitation (0.47) and latitudinal range mid-point (–0.61).

Analysis

We analysed introduction as a binary trait. We did not address variation in the number of introductions because it is difficult to get good data on the number of introductions, especially for species that have been accidentally translocated. We adopted both taxonomic and phylogenetic approaches to assess non-randomness in the characteristics of introduced mammal species. All analyses were conducted in R v. 3.1.1 (R Core Team 2014).

We used the permutation approach described in Blackburn and Cassey (2007) to test for differences between the observed number of introduced mammal species in each mammalian order, and the number that would be expected if mammals were selected at random for introduction. Each iteration of the simulation involved picking S species at random, and without replacement, from the global mammal fauna, using the *sample* function in R, and summing the number of these randomly chosen species in each order. S is the number of mammal species we recorded as having been introduced ($S = 306$; see Results). This was repeated 100,000 times, to produce 100,000 lists of randomly chosen species. The observed number of species actually introduced from any given mammal order was judged significantly greater than expected if at least 99.95% of the randomly derived values for that order were less than the observed (i.e., if there were fewer species from that order on 99.95% of the 100,000 random lists). Similarly, the observed number of introduced species was judged to be significantly less than expected if at least 99.95% of the randomly derived values for that order were greater than the observed (i.e., if there were more species from that order on 99.95% of the 100,000 random lists). These percentages were chosen to be conservative, being less than the Bonferroni corrected critical value of $a/n = 0.0017$; where $a = 0.05$ and $n = 29$ (the number of mammal orders). The same simulation approach was also used to assess taxonomic selectivity in terms of family membership. In this case, we used percentages of 99.995, given 153 mammal families.

We used phylogenetic logistic regression (Ives and Garland 2010) and the mammalian phylogeny in Fritz and Purvis (2010) to test whether or not introduced mammals differed from other mammal species in terms of the life history, ecological, distributional and environmental variables described above. We calculated the phylogenetic statistic *D* (Fritz and Purvis 2010), using the phylo.d function in the R package 'caper' (Orme et al. 2013), to test for phylogenetic signal in whether or not species in this sample had been introduced. *D* measures character dispersion on a phylogeny: a value of 0 indicates that the trait is clumped as if it had evolved through Brownian motion, and a value of 1 that the trait is randomly dispersed across the phylogeny (Fritz and Purvis 2010). We fitted univariate phylogenetic logistic regression models (Ives and Garland 2010) using the phylolm function in the 'phylolm' package, with the error term modelled on the basis of the estimated Pagel's λ (Ho and Ane 2014). We then fitted a full model for mammal species for which there were no missing data in the variables found to be significant in the univariate tests. We calculated Variance Inflation Factors for these variables using standard linear and PGLS models to test for collinearity amongst these predictors. Variable significance in the full model was assessed on the basis of full model estimates (beta) and their standard errors (Hegyi and Laczi 2015). The variance explained by this model was estimated using Nagelkerke's R^2 (Nagelkerke 1991). Adult mass, litter size, maximum longevity, geographic range size, and precipitation were all natural logarithmically transformed for this analysis, while human population density was natural log + 1 transformed.

Results

We identified a total of 306 mammal species that have been recorded as having been introduced to areas beyond the limits of their normal geographic distributions (Suppl. material 1). These represent 5.65% of all mammal species in the taxonomy used here.

Six mammalian orders have had more species introduced outside their native range limits than expected by chance (Table 2). Of these, Diprotodontia, Artiodactyla, Perissodactyla and Carnivora have had significantly more introduced than expected after Bonferroni correction for multiple tests. The order with the most introduced mammal species is Artiodactyla, with 83 (34.7%). Within this order, five families also have had more introduced species than expected (Table 3), and of these, the Bovidae and Cervidae remain significant after Bonferroni correction. The Bovidae has had the most species introduced of any mammalian family, with 49 (Table 3). The Carnivora, Diprotodontia and Perissodactyla each have one family that is significantly over-represented in the list of introduced mammals after Bonferroni correction (the Mustelidae, Macropodidae and Equidae, respectively; Table 3).

The mammalian order with second highest number of introduced species is the Rodentia, with 75 (Table 2). However, this is actually significantly fewer species than expected, even after Bonferroni correction, given the very high richness of this order (Table 2). Two Rodent families, the Cricetidae and Muridae, also have fewer intro-

Table 2. The distribution, across mammal orders, of all mammal species (No. species), introduced mammal species (No. introduced), and the expected number of introduced species per order (median and range, based on 100,000 iterations of the permutation test) assuming that mammal species were selected for introduction at random (Expectation). Species numbers are based on the taxonomy in Wilson & Reeder (2005). Orders with significantly more introduced species than expected by chance are shown in bold, while orders with significantly fewer introduced species are shown in italics.

Order	No. Species	No. Introduced	Expectation
Afrosoricida	51	1	3 (0–12)
Artiodactyla	239	**83*****	**13 (2–32)**
Carnivora	286	**41*****	**16 (3–34)**
Cetacea	84	*0**	*5 (0–17)*
Chiroptera	1116	*3****	*63 (33–98)*
Cingulata	21	2	1 (0–9)
Dasyuromorphia	71	1	4 (0–14)
Dermoptera	2	0	0 (0–2)
Didelphimorphia	87	3	5 (0–15)
Diprotodontia	143	**28*****	**8 (0–22)**
Erinaceomorpha	24	2	1 (0–8)
Hyracoidea	4	0	0 (0–4)
Lagomorpha	92	**12***	**5 (0–17)**
Macroscelidea	15	0	1 (0–6)
Microbiotheria	1	0	0 (0–1)
Monotremata	5	2	0 (0–4)
Notoryctemorphia	2	0	0 (0–2)
Paucituberculata	6	0	0 (0–4)
Peramelemorphia	21	2	1 (0–8)
Perissodactyla	16	**6****	**1 (0–7)**
Pholidota	8	0	0 (0–5)
Pilosa	10	1	0 (0–5)
Primates	376	30	21 (6–41)
Proboscidea	3	**2***	**0 (0–3)**
Rodentia	2277	*75****	*129 (89–168)*
Scandentia	20	0	1 (0–9)
Sirenia	5	0	0 (0–4)
Soricomorpha	428	*12***	*24 (7–46)*
Tubulidentata	1	0	0 (0–1)

*P<0.05, **P<0.01, ***P<0.0001.

duced species than expected after Bonferroni correction (Table 3). Conversely, the Castoridae, Hystricidae and Sciuridae have had more species than expected introduced, albeit that these are not significant once corrected for multiple tests (Table 3). A further three mammalian orders have also had fewer than expected species introduced, of which Chiroptera and Soricomorpha remain significant after Bonferroni correction (Table 2). Five Chiropteran families have had fewer species introduced than expected

Table 3. The distribution, across mammal families, of all mammal species (No. species), introduced mammal species (No. introduced), and the expected number of introduced species per family (median and range, based on 100,000 iterations of the permutation test) assuming that mammal species were selected for introduction at random (Expectation). Species numbers are based on the taxonomy in Wilson and Reeder (2005). Only families with significantly more (in bold) or fewer (in italics) introduced species than expected by chance are shown.

Order	Family	No. species	No. Introduced	Expectation
Artiodactyla	**Bovidae**	143	**49*****	8 (0–21)
	Camelidae	4	**4*****	0 (0–4)
	Cervidae	50	**19*****	3 (0–13)
	Suidae	19	**5****	1 (0–7)
	Tayassuidae	3	**2***	0 (0–3)
Carnivora	**Canidae**	35	**8****	2 (0–10)
	Mustelidae	59	**14*****	3 (0–12)
	Viverridae	35	**7****	2 (0–10)
Chiroptera	*Hipposideridae*	81	*0**	4 (0–16)
	Molossidae	100	*1**	6 (0–19)
	Phyllostomidae	160	*0****	9 (0–23)
	Pteropodidae	186	*1***	10 (0–28)
	Vespertilionidae	407	*0****	23 (6–45)
Diprotodontia	**Macropodidae**	65	**16*****	4 (0–13)
	Potoroidae	10	**3***	0 (0–5)
	Vombatidae	3	**2***	0 (0–3)
Lagomorpha	**Leporidae**	61	**12****	3 (0–13)
Perissodactyla	**Equidae**	7	**5*****	0 (0–4)
Primates	**Cercopithecidae**	132	**14***	7 (0–20)
	Lemuridae	19	**6****	1 (0–8)
Proboscidea	**Elephantidae**	3	**2***	0 (0–3)
Rodentia	**Castoridae**	2	**2****	0 (0–2)
	Cricetidae	681	*12****	38 (16–66)
	Hystricidae	11	**3***	0 (0–6)
	Muridae	730	*17****	41 (20–69)
	Sciuridae	278	**25***	16 (2–33)
Soricomorpha	*Soricidae*	376	*10***	21 (5–42)

*P<0.05, **P<0.01, ***P<0.0001

by chance, and the Phyllostomidae and Vespertilionidae remain significantly underrepresented after Bonferroni correction (Table 3).

Introduced species are distributed across the mammal phylogeny with $D = 0.51$. This was significantly different from both phylogenetic randomness ($P < 0.0001$) and a strict Brownian motion model of evolution ($P < 0.0001$). Univariate phylogenetic logistic regressions show that introduced species have significantly larger body masses and litter sizes, longer lifespans and broader diet breadths than mammal species not introduced (Table 4). Introduced mammal species have much larger native geographic

Table 4. Univariate phylogenetic generalised logistic models of the relationship between mammal species introduction and the variables in the second column. Ch. = characteristic of interest with which each variable is associated (see Introduction, Methods, and Table 1). Negative values of latitude relate to latitudes in the southern hemisphere. Negative values of longitude relate to longitudes west of the Greenwich Meridian. Estimate ± s.e. = regression coefficient ± standard error, Log. = natural logarithmically transformed, Lat. = Latitude, Long. = Longitude, Pop. = Population. λ = maximum likelihood estimate of Pagel's lambda for the model.

Ch.	Variable	Estimate ± s.e.	t	N	P	λ
1	Log. Adult Body Mass	0.029 ± 0.004	7.44	3435	< 0.0001	0.44
2	Log. Litter Size	0.092 ± 0.016	5.62	2460	< 0.0001	0.43
3	Log. Maximum longevity	0.152 ± 0.023	6.63	1000	< 0.0001	0.53
4	Diet Breadth	0.013 ± 0.004	2.95	2114	0.003	0.46
4	Habitat Breadth	0.013 ± 0.012	1.12	2664	0.26	0.52
5	Trophic Level	–0.025 ± 0.013	–1.86	2114	0.06	0.43
6	Log. Geographic range size	0.014 ± 0.001	11.19	4457	< 0.0001	0.43
7	Log. (1+Human Pop. Density)	0.008 ± 0.003	2.80	4457	0.005	0.43
8	Lat. range mid-point	0.0017 ± 0.0002	7.70	4457	< 0.0001	0.42
8	Long. range mid-point	–0.0001 ± 0.00007	–1.47	4457	0.14	0.43
8	Log. Precipitation	–0.028 ± 0.005	–5.25	4336	< 0.0001	0.44
8	Temperature	–0.0005 ± 0.00006	–8.73	4336	< 0.0001	0.43

Table 5. The full phylogenetic generalised logistic model based on the significant variables in Table 4. The estimate and standard error for temperature are based on units of 0.1°C. Nagelkerke's R^2 = 0.30; N = 704, maximum likelihood estimate of Pagel's lambda = 0.32.

Variable	Estimate	Std. Error	t	P
Intercept	–1.08	0.238	–4.52	<0.0001
Log adult body mass	0.046	0.010	4.58	<0.0001
Log. Litter Size	0.140	0.040	3.50	0.0005
Log maximum longevity	0.099	0.031	3.21	0.0014
Diet Breadth	0.009	0.009	0.95	0.34
Log geographic range size	0.049	0.008	5.74	<0.0001
Log. (1+Human Pop. Density)	0.046	0.015	3.13	0.002
Lat. range mid-point	0.0009	0.001	1.01	0.31
Precipitation	–0.029	0.025	–1.16	0.24
Temperature (0.1°C)	–0.001	0.0003	–4.38	<0.0001

ranges (Table 4): the geometric mean range size of introduced mammals is 8.5 times larger than the mean of species that have no recorded introductions. Introduced mammal species also tend to originate from significantly further north, from cooler areas, from areas with lower precipitation, and from areas with higher human population densities, than mammal species with no recorded introductions (Table 4). Conversely, mammal species with or without recorded introductions showed no difference in their longitudes of origin, habitat breadths or trophic levels (Table 4).

The full phylogenetic logistic regression model, for the subset of 704 (of which 178 were introduced) species for which data on all nine significant variables in Table 4 were available, included strong positive effects of adult body mass and geographic range size, and a strong negative effect of temperature (Table 5). There were also positive effects of litter size, maximum longevity, and human population size. Variance inflation factors for these nine variables ranged from 1.06 to 2.27 using standard linear models (and were lower using PGLS models), indicating low levels of collinearity.

Discussion

The geographic distributions of species have always been dynamic, but in recent centuries the processes underlying these changes in distribution have been greatly accelerated. In particular, natural dispersal, which for most of the history of life has been the only way in which species expand their ranges, has been massively augmented by the global movement of organisms by human activities. The first recorded human-introduction relates to a mammal–the grey cuscus *Phalanger orientalis* introduced to New Ireland around 20,000 years ago (Grayson 2001)–and given the general interest in both biological invasions and mammals, it is surprising that only one previous study (Capellini et al. 2015) has attempted to quantify or characterise the world's introduced mammal fauna. The work reported here takes significant further steps in these regards. First, we identify a larger set of mammal species with introduced populations than in previous studies. Second, we characterise for the first time the taxonomic composition of introduced mammal species, and identify which orders and families have more introduced species than expected by chance. Third, we analyse a wide set of traits that may influence which species have been introduced at the global scale. These data reveal clear evidence of selectivity in the identities and traits of introduced mammal species worldwide, as has previously been demonstrated for birds and amphibians (Blackburn et al. 2009; Tingley et al. 2010).

Our database includes 306 species that we considered to have been introduced somewhere in the world, which is just under 6% of all mammal species. Mammals therefore sit between birds (c.10%; Blackburn et al. 2015) and amphibians (c.3%; Tingley et al. 2010) in terms of the proportion of their global richness species subject to human-mediated introduction. It is also 74 (32%) more species than in another recent global compilation (Capellini et al. 2015). These two compilations share 215 species in common, but each included some species not on the other list. The greater number of species on our list reflects in part the fact that our literature search identified species that we believe have unambiguously been introduced (e.g. *Callosciurus erythraeus*; Bertolino and Lurz 2013), but in part also differences of interpretation of the evidence for introduction, especially in terms of whether or not a population counted as an introduction versus a re-introduction. The temporal dynamics of native distributions means that this judgment is not always black-and-white.

For example, there is little doubt that the Barbary ape (*Macaca sylvanus*) population on Gibraltar derives from individuals liberated by humans (other individuals were released in Germany; Long 2003), but this species was widespread across Europe and North Africa in the Pleistocene. Its historic distribution spanned much of North Africa, though it persists in only a few parts of this former range. Capellini et al. (2015) did not include this species as having been introduced, but we followed the IUCN (http://www.iucnredlist.org/details/summary/12561/0) and included it. Arguably, this species is a "restored native" *sensu* Crees and Turvey (2015), rather than a non-native, but the degree to which the German introduction location in particular could be considered within the potential current distribution of the species (and hence a re-introduction) is open to debate. In other cases, it is not clear whether the introduction location was actually within the previous range of the species. For example, the individuals of the Black Capuchin (*Sapajus* (*Cebus*) *nigritus*) released on Anchieta Island (Bovendorp and Galetti 2007) are beyond this species' range limits as given by the IUCN (http://www.iucnredlist.org/details/136717/0). Nevertheless, Anchieta is offshore from that range, and so it is plausible that the Black Capuchin could once have been native there, although there is no evidence of this. As the population definitely derives from captive individuals and lacking evidence that the species had ever previously inhabited the island, we again included this species on our list of introductions. In sum, as noted earlier, we included species as introduced when individuals arrived into an environment via human mediation, unless there was evidence that the environment was within the historic range of the species.

The mammalian order with the most introduced species globally in our database is the Artiodactyla: this order includes less than 5% of all mammal species, but 27% of all introduced species (Table 2). This representation is much higher than expected by chance. Artiodactyls include deer (Cervidae), camels and their relatives (Camelidae), antelopes, buffaloes, sheep and goats (Bovidae), pigs (Suidae), and peccaries (Tayassuidae), and therefore the most important animals for most human societies in terms of meat, game, milk, fibres (wool and hair), hides and transport (Pattiselanno 2003; Geisser and Reyer 2004; Haenlein 2001; Haenlein 2007). It is unsurprising that humans should have desired to introduce such species to new areas, so that they could continue to benefit from the goods and services provided by them. Classic examples include: (i) the release of pigs and goats onto islands by European sailors, to ensure a supply of meat the next time they (or other people) made landfall there (Cheke 2010; Campbell and Donlan 2005; Robins et al. 2003); (ii) the introduction by Acclimatization Societies of a range of game species (e.g., deer) to provide hunting on naturally mammal-free New Zealand (McDowall 1994); and (iii) the introduction of camels to aid with the exploration and development of the newly colonised (by Europeans) desert continent of Australia (McKnight 1969; Long 2003). The Bovidae, Camelidae, Cervidae, Suidae and Tayassuidae are all significantly over-represented on the list of mammal introductions, and the Bovidae and Cervidae remain so when correcting for multiple comparisons (Table 3).

The mammalian order with the second highest number of introduced species globally is the Rodentia (75 species, 24.5%; Table 2). This order includes some of the most

ubiquitous and notorious alien species, such as black and brown rats (*Rattus rattus* and *R. norvegicus*, respectively) and the house mouse (*Mus musculus*), which have been accidentally introduced to most ice-free land areas on the planet. However, not all rodent introductions are accidental: many species have been introduced deliberately for a variety of reasons, such as Pacific rats (*R. exulans*) for food (Roberts 1991; Matisoo-Smith et al. 1998), beavers (*Castor* sp.) for fur (Lizzaralde 1993), and the grey squirrel (*Sciurus carolinensis*) for ornamentation (Huxley 2003; Gurnell 1996). Nevertheless, given that Rodentia is the richest mammalian order, with more than 40% of all the world's mammal species, the 75 introduced species actually equates to significantly fewer than would be expected by chance (Table 2). The major families within the Rodentia (Cricetidae and Muridae) are also significantly under-represented (Table 3). Presumably, few rodents have qualities that would promote their deliberate introduction, or the opportunity for accidental introduction (see below). The second richest mammalian order (Chiroptera) is also significantly under-represented on the list of introduced species (Table 2), as are five of its families (Table 3), as only three (<1%) of the 1,116 bat species have recorded introductions.

Other mammalian orders well represented on the global list of alien species include Carnivora (41 species, 13%) and Diprotodontia (28 species, 9%) (Table 2). Amongst introduced Carnivora, the Mustelidae, Viverridae and Canidae figure prominently. The first of these includes a variety of stoat and weasel species often introduced for the purposes of pest control–sometimes as a misguided response to problems caused by introduced rodents (Uchida 1968; Uesugi et al. 1998). Introduced Diprotodontia include a number of translocations to offshore islands for the purposes of conservation, again largely in response to problems caused by other introduced species (Langford and Burbidge 2001; Miller et al. 2011), but also introductions for food (e.g. *P. orientalis* mentioned above), fur (*Trichosurus vulpecula* to New Zealand) and through escapes from private collections (e.g., *Macropus rufogriseus* in the UK) (Long 2003). The order Perissodactyla is also significantly over-represented amongst introduced species (Table 2), due to the introduction of most of the species in the family Equidae (Table 3), for similar reasons to the Artiodactyla (see above).

As well as exhibiting significant selectivity in terms of identity, introduced mammals are a non-random set in terms of their traits (Table 4). The relative over-representation of species introduced for game, pack, fur, or other goods and services, translates into a strong relationship between introduction and body size: the geometric mean mass of introduced mammals is 24 times that of species that have no recorded introductions. Introduced species also tend to be longer-lived and to have larger litters, as also shown by Capellini et al. (2015), which is not simply a consequence of allometry, as maximum longevity, litter size and body mass all explained variation in introduction status in a phylogenetic multivariate model (Table 5). Capellini et al. (2015) found an effect of number of litters per year but not body mass on introduction; we do not use the former measure as it lacks data relative to litter size, but a correlation between these two variables may explain the effect of body mass in our full model. Interestingly, running our phylogenetic models on Capellini et al.'s (2015) list of introduced mammals revealed

a similarly strong univariate effect of body mass on introduction, but a much weaker effect in the full model (estimate ± standard error = 0.021 ± 0.009, t = 2.33, P = 0.02; c.f. Table 5). This suggests the weaker effect of mass in their analysis is not simply an effect of their inclusion of number of litters per year. Jeschke and Strayer (2006) found univariate effects of longevity and body size on a much smaller sample of mammal species introductions to Europe and North America, but only longevity (and trophic level) explained variation in their phylogenetic multivariate model. The benefits to humans of large body size and litter size in introduced species are obvious; the additional independent benefits of longevity are less so, although such species may be better able to survive the introduction process. Our global dataset also identifies a tendency for introduced species to have broader diet breadths than expected (Table 4), although there was no effect of diet breadth on introduction in the full model (Table 5).

Species traits help determine which mammals have been introduced, but so too do the characteristics of their geographic range: widespread species inhabiting cooler locations and areas with denser human populations are more likely to have been introduced (Tables 4, 5). These results identify an effect of species availability on selection. Widespread mammal species tend also to be abundant (Blackburn et al. 1997), and hence are likely to be more familiar to local inhabitants, and more available for deliberate or accidental translocation. Availability will also be higher for species that overlap areas with higher human population densities. Similar patterns have been observed for global bird (Blackburn et al. 2009) and amphibian (Tingley et al. 2010) introductions, and in multi-taxon models for mammal, bird and fish introductions to Europe and North America (Jeschke and Strayer 2006). The negative effect of temperature (and precipitation in univariate analysis) likely reflects the fact that much of the history of introductions has occurred alongside movements of species by Europeans to and from Europe and the neo-European colonies (e.g. especially North America, Australia, New Zealand, South Africa), which tend to lie at temperate latitudes. Peoples from these latitudes moved the species that were available to them. Translocations are still occurring at these latitudes, although increasingly they concern native species moved for conservation purposes (e.g. threatened marsupial species in Australia (Masters et al. 2004), declining game species in southern Africa (Matthee and Robinson 1999; Spear and Chown 2009), or on-going unplanned introductions as a result of releases or escapes of mammals from the pet trade (e.g., domestic cats (*Felis catus)* in several countries, including Australia (Abbott 2002) and New Zealand (Parkes and Murphy 2003).

Phylogenetic analysis revealed that there is significant phylogenetic signal in which mammal species have been introduced, albeit less than expected under a Brownian motion model of evolution. This reflects the clear non-randomness of introduction with respect to taxonomic affiliation, but that selection is not simply based around phylogenetic clumping of mammals. These models demonstrate that several variables explained independent variation in introduction (large-bodied, long-lived, widespread, temperate species), in line with findings from other taxa at the global or regional scale (Jeschke and Strayer 2006; Blackburn et al. 2009; Tingley et al. 2010; van Wilgen et al. 2010; García-Díaz and Cassey 2014). Nevertheless, these models also show that

most of the variation in introduction is unaccounted for: the full model for our data explained c. 30%. We suspect that much of the unexplained variation relates to the intrinsically stochastic nature of the introduction process, driven as it is by historical contingency in the interaction between the evolutionary history of mammals that located certain species with certain traits in the way of human histories of movement and demands for goods and services.

Introduction is an early step on the invasion pathway (Blackburn et al. 2011), and the characteristics of the species that get introduced outside their normal distributions determine which traits are available to influence the subsequent stages of establishment and invasive spread. Our analyses show that the species selected by humans to face the challenges of these later invasion stages tend to be long-lived, large-bodied, and fecund; they also tend to be widespread and come from areas with higher human population densities (Tables 4, 5). Widespread species may be able to tolerate a broad range of environmental conditions (Gaston 2003), and the fact that they are likely to be moved to areas with high human population densities, as well as from such areas, increases the likelihood that they will find new locations to their liking (Blackburn et al. 2009). Large-bodied, long-lived species may be less susceptible to the negative effects of demographic and environmental stochasticity (Sæther et al. 2004), whereas rapidly reproducing species can quickly escape the demographic and environmental traps associated with small populations (Moulton and Pimm 1986). This suggests that, deliberately or inadvertently, people have chosen alien mammal species with characteristics that may predispose them to success in the later stages of invasion.

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Supplementary material 1

A list of introduced mammal species

Authors: Tim M. Blackburn, Sally L. Scrivens, Sarah Heinrich, Phillip Cassey

Data type: Text

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Supplementary material 2

References from which the database of introduced mammals was constructed

Authors: Tim M. Blackburn, Sally L. Scrivens, Sarah Heinrich, Phillip Cassey

Data type: Text

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